

Scientific note**Ice age tropical South America: What was it really like?**

by

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Reading the article by HAFFER & PRANCE (2001) and then a reply (rebuttal) by COLINVAUX et al. (2001) gives one the feeling that something is going wrong in the discussion. The evaluation by HAFFER & PRANCE is an honest and respectful analysis of the status of the various theories proposed to explain aspects of Amazonian biodiversity and biogeography using the data provided by colleagues specialized in other fields. Honest disagreements may exist on the conclusions because of the uncertainty created by the fact that nobody was present to see what really happened in the distant past. This is the general problem with paleo-data and their interpretation, but as in the case of the climatic significance of stone lines, when most people agree on a certain interpretation, we may employ it carefully. Paleoecologists can use several independent kinds of data to increase the probability that their conclusions are correct. If three different sets support the same interpretation and one does not, the probability that the three are right is relatively high. Interpretation of paleo-data requires great honesty and objectivity, as they are easy to manipulate consciously or unconsciously and scientific discussion is an important safeguard. Scientific theories and hypotheses constitute possible explanations of particular facts. They are important for directing research that may falsify or confirm them. A good theory or hypothesis should be falsifiable and the refuge theory is a good example. By contrast, it seems to me that the glacial disturbance theory is not falsifiable and thus cannot make an important contribution to the discussion.

COLINVAUX et al. state that paleoecological data falsify the Amazonian refuge theory and that it has to be "discarded". Is that true? A careful analysis of their article shows that, although there are good discussions of some of the themes, their conclusions are often based on a biased interpretation of the data. They repeatedly attempt, in what

* Dedicated to Prof. Dr. Harald Sioli on the occasion of his 90th anniversary.

I consider an unacceptable way, to discredit data that do not fit their theory of vegetational stability and they ignore other important conflicting evidence. Their accusation that the interpretations of researchers in different fields were biased to a certain extent by the Amazonian refuge theory also applies to them.

There is no doubt that all those who have worked in and published on Amazonia have learned a lot and have changed their views to a certain extent during the course of the past 20 years or so. The original picture of small patches of forest in an extensive sea of pure grass savanna is probably not the correct ice-age scenario. There could equally have been large areas of forest partly separated by a cerrado type of vegetation and/or open savannas, or locally or temporarily wet forested areas separated by dry forest. The latter scenario is the one now favored for the general region, consisting of "refuge areas" for wet-forest species and others for dry-forest species. If the climate became drier, wet forest may have become dry forest and dry forest may have become cerrado or savanna. We are all now convinced that the climate was drier and colder during certain intervals in the Last Glacial (even COLINVAUX et al. agree). We can produce general estimates of the degree of change, but we need more reliable data to establish when, where, and how long the changes occurred. The ice-age climate was not uniform in time, as we know from the Andean region and also from several points in Amazonia. There were strong temporal fluctuations in rainfall and temperature. Therefore, we cannot use data from 20,000 BP at one site and 35,000 BP at another to reconstruct a single scenario for vegetation and climate. Besides, we should never forget that Amazonia is not climatologically homogeneous and especially that there are considerable differences in intensity and seasonality. Consequently, if we are trying to reconstruct and discuss glacial-time Amazonian vegetation and climate, we must specify the "time-slice". Although much of the Last Glacial shows climatically intermediate situations, to understand what happened we need to know the extreme situations, i.e. the Last Glacial Maximum (LGM) and similar earlier extremes.

In a recent publication, we gave a critical review of the interpretations of the sites providing palynological or other climatologically important information (VAN DER HAMMEN & HOOGHIEEMSTRA 2000). COLINVAUX et al. cite that publication on one occasion, but apparently did not read it carefully since they do not cite the most important data or interpretations. They assert incorrectly that the general reduction of rainfall we estimated was based only on the fluctuations in the Carajás lake level. On the contrary, it was based on all available data on lake-level fluctuations during the LGM. Moreover, they try to invalidate the relevance of the Carajás pollen diagram and sediment analysis on the basis that it represents only local vegetation. Instead, our interpretation was based on a study of the recent local and regional vegetation and pollen rain. There are both a local and a regional signal in the pollen diagrams. Some 60 % of the recent and Late Holocene pollen rain on the plateau was not from the vegetation on the plateau, but from the forest around and below the plateau. The interpretation of pollen diagrams should be based on this type of information and should not be guided by "wishful thinking", as COLINVAUX et al. do in several places to argue that their theory is correct.

Another example of their procedure is the treatment of the first data published on changes in the Amazonian rainforest vegetation at the Katira site in Rondonia. The pollen data show replacement of rainforest by grass savanna (practically without trees) around 18,000 BP. There are only a few samples, but three kinds of independent data

confirm the conclusion: (1) pollen data (2) changes in the delta ^{13}C values of the organic matter in the sediments (presence of C3 plants during the rainforest phase and C4 plants, mainly tropical grasses, during the savanna phase) and (3) a change to colluvial sediments during the savanna phase, indicating incomplete vegetation cover on the soil. These are really hard data. COLINVAUX et al. only state that the site is "no more than 100 km" from the rainforest border and that the number of samples is low. They "forget" this evidence in their conclusions.

Other important early data come from the coastal sediments of Guyana and Surinam, where typical dry grass-savanna existed during glacial lowering of the sea level. This evidence is not mentioned at all. Another example of this manner of treating data is that provided by the dune fields. Those of the Rio Branco-Rio Negro region are well documented by respected scientists and are located where they would be expected in the case of decreasing rainfall in the heart of Amazonia. Although there may have been recent revivals under the influence of natural or anthropogenic disturbances, this qualification applies to all fossil dune areas. They state that there are no dates for the dunes on the Llanos of Colombia and Venezuela, although we cite Late Glacial dates in our publication.

Among the most impressive available data are changes in the lake levels at Carajás, Pata, and Maicuru, all of which dried up completely during several millennia around the LGM. As a consequence, there is no sediment or pollen record for that interval and no data on the vegetation during that time of extreme climatic conditions. Drought extended between approximately 25,000 and 15,700 BP at Macuiru, approximately 31,000 and 18,000 at Pata, and approximately 23,777 and 12,520 BP at Carajás. A similar LGM hiatus indicating drying up of lakes has been documented west, north, and south of Amazonia (Fuquene, Valencia, Salitre). Only one conclusion can be drawn from all this evidence: the driest millennia (possibly lasting some 10,000 years) occurred around the LGM and are not represented in pollen diagrams. Sediments below and above this dry interval were deposited during relatively wetter conditions.

Since the evaporation rate in Amazonia is known or can be reliably estimated, it is possible to infer the rainfall at a particular location. If no leakage or inflow of water is occurring, we can calculate how much reduction in precipitation would be required to dry up the lake. Leakage would result in too high an estimate and inflow in one that is too low. As the lakes studied have a rather thick deposit of clay and other impermeable sediment, leakage would have been zero or very limited. Inflow of surface water from the surroundings is more probable and lower temperatures would reduce the rate of evaporation, making estimates of minimal reduction of rainfall likely to be too low rather than too high. The estimates for reduction of rainfall at the above-mentioned sites are very similar and mostly in the range of 40-60 % (more than 30 % at Carajás). So it seems probable that there was a general reduction in precipitation of at least 40-50 % during several millennia around the LGM, which would have created a drought crisis. A general reduction seems to have prevailed over most of tropical South America, although there were certainly local differences. This decrease during the Upper Pleniglacial (LGM period) is a nearly world-wide phenomenon that seems to be related to lowered sea and air temperatures and changes in coastlines as a result of the decline of more than a hundred meters in sea level.

As to interpretation of the Amazon fan sediments, the following considerations are important. River and estuarine sediments frequently contain considerable quantities of

reworked organic material including pollen, which produce excessively old ^{14}C ages (as in the Holocene sediments of Marajó Island). During the LGM, when sea level was more than a hundred meters lower, the Amazon River cut its valley deeply into the earlier sediments of the Middle Pleniglacial wet period and the last interglacial. Millions of tons of these reworked older sediments were deposited on the fan. The pollen in these sediments therefore does not reflect the contemporary vegetation correctly. Rather, it represents for the most part pollen redeposited from earlier periods. However, the high values of fern spores provide an interesting signal for which we as yet have no explanation. We need much more detailed chronological evidence than now exists.

Another attempt by COLINVAUX et al. to get rid of evidence that seems to indicate important changes in the vegetation is their curious discussion of the fossils of large grazing herbivores in the upper Juruá-Purus area. Transportation of the large fossils from higher elevations may have occurred in the relatively steep upper part of some rivers, such as the Napo, but is most unlikely for the extensive low areas. So another strange scenario is created, in which animals from the Andes somehow became displaced and subsisted on grasses along the river shores. If we plot the Acre finds on the map of possible Amazonian vegetation during the estimated reduction of rainfall, however, there is a striking coincidence between most of the fossil beds and the area inferred to have had "savanna or cerrado vegetation and dry, deciduous or savanna forest" (Fig. 1). This coincidence seems to confirm the view expressed by the original authors (see KRONBERG & BENCHIMOL 1993; RANCY 1993).

Superimposing the estimated 40 % reduction in precipitation on the present-day rainfall distribution in Amazonia and assuming the extant correlation between rainfall and vegetation produces the pattern shown on Figure 1. The vegetation reconstructed from all the pollen profiles agrees with this pattern (Guyana, Surinam, Carajás, Katira, Aracuara, Mera, and San Juan Bosco). The Lake Pata sequence, published after an earlier version of the map was produced, also fits, as do the locations of the dune fields. This independent confirmation increases confidence in the results, but is neglected by COLINVAUX et al. We do not consider this map correct in detail because it depends on the accuracy of the modern map of rainfall distribution and the correctness of the estimated decrease in rainfall during the LGM. It will certainly need correction as new paleo and recent evidence become available.

Although COLINVAUX et al. now admit that the LGM climate was drier, they insist curiously that there was no Amazonian aridity. As we have indicated, the three diagrams of lake sediments all show a hiatus in sedimentation lasting thousands of years, corresponding approximately to the LGM. This period of low rainfall has no pollen record and hence no conclusions can be drawn from the profile on the type of vegetation that existed during this period. This omission is not taken into account in inferring the continuous existence of forest.

The proposal to discard the refuge theory is unacceptable since the existing geological and paleoecological data in no way falsify it. Instead, these data strongly suggest that the vegetation pattern during the LGM provided sufficient differentiation to permit isolation among local populations, as occurs in less extreme form today when wet forest areas with high biodiversity are separated by drier forest areas with much lower biodiversity. Much remains to be discovered and studied, some of which may confirm or change our views. Aggressive defense of preferred interpretations neither encourages their acceptance nor improves the data base. Let us be careful in interpreting the still

scanty evidence and let us also treat respectfully the serious work and honest conclusions of our colleagues.

References

For a more complete treatment of the items discussed here, refer to the following publication:

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